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Dynamic mimicry in an Indo-Malayan octopus

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During research dives in Indonesia (Sulawesi and Bali), we filmed a distinctive long-armed octopus, which is new to science. Diving over 24 h periods revealed that the ‘mimic octopus’ emerges during daylight hours to forage on sand substrates in full view of pelagic fish predators. We observed nine individuals of this species displaying a repertoire of postures and body patterns, several of which are clearly impersonations of venomous animals co-occurring in this habitat. This ‘dynamic mimicry’ avoids the genetic constraints that may limit the diversity of genetically polymorphic mimics but has the same effect of decreasing the frequency with which predators encounter particular mimics. Additionally, our observations suggest that the octopus makes decisions about the most appropriate form of mimicry to use, allowing it to enhance further the benefits of mimicking toxic models by employing mimicry according to the nature of perceived threats.

Keywords: mimic octopus; dynamic mimicry; cephalopod; crypsis; mimicry; polymorphism; predator defence

1. INTRODUCTION

Camouflage and mimicry are well documented in cephalopods (Hanlon & Messenger 1996). Although other species impersonate low-value or difficult-to-catch models, until now no cephalopod was known to impersonate poisonous or distasteful animals. Furthermore, no animal of any group has previously been described that is able to switch back and forth between mimicry of different model organisms.

The ‘mimic octopus’ has an arm span of up to 60 cm, and was discovered in 1998 off the coast of Sulawesi, Indonesia. It appears to be restricted to the Indo-Malayan archipelago, and a formal description is currently in process (Norman & Hochberg 2001). It is found on silt and sand substrates off river mouths in water between 2 m and 12 m deep. This habitat is rich in benthic infauna with a high activity of worms, echinoderms, crustaceans and fishes, riddling the sea-floor with burrows, tunnels and mounds.

2. METHODS

During daylight dives off the northern coast of Sulawesi and in Gilimanuk, Bali, we observed nine adult mimic octopuses over a total of 16 days (between October 1998 and October 2000). Still photographs and over 6 h of video footage of this octopus species were obtained. Figure 1 shows still images of various behaviours and the proposed mimicry models. These are intended to give an indication of the body postures associated with the behaviours we describe, but cannot convey the movements that are the most convincing aspect of these displays. Our video of these behaviours has been incorporated into a recent natural-history documentary (BBC/Discovery 2000) and samples are provided on The Royal Society’s Web site (electronic Appendix A).

3. RESULTS

Mimic octopuses were typically encountered sitting in the mouths of burrows on sand or silt mounds (figure 1*a*). Foraging individuals typically crawled along the substrate in drab brown colours (figure 1*b*), using their arm tips to probe down holes and the flared webs to trap fleeing prey. When moving faster (using jet propulsion), the octopus drew all its arms into a leaf-shaped wedge with a central mantle trailing the head (figure 1*c*). In this form it swam between worm mounds, undulating the body in the fashion of a swimming flatfish. We believe that this unique posture is mimicry of an abundant sole found in this habitat (*Zebrias* spp., figure 1*d*). Four individuals were also observed swimming just above the sea-floor with arms trailing from the body, taking on the appearance of a lion-fish (*Pterois* spp., figure 1*f*) swimming with its banded poisonous spines fully flared. Figure 1*e* is the closest image we have to this behaviour. On four occasions, attacks by small territorial damselfishes (*Amphiprion* spp.) elicited a posture where six arms were threaded down a hole and two were raised in opposite directions, banded, curled and undulated (figure 1*g*), to produce the appearance of a banded sea-snake (*Laticauda* sp.) (figure 1*h* and Quicktime clip in electronic Appendix A). The majority of individuals also used general background camouflage patterns in response to certain passing predatory fishes (such as the trevally *Gnathodon speciosus*). Other distinctive behaviours were observed, including sitting on top of sand mounds and raising all the arms above the body, each arm being held in a zigzag form. It is possible that this posture impersonates large solitary sand anemones (such as *Megalactis* spp.) that are armed with powerful stinging cells (nematocysts). In another incident, a large female (arm span, 60 cm) swam to the sea surface from 4 m deep, then slowly sank with undulating arms spread evenly around the animal. This

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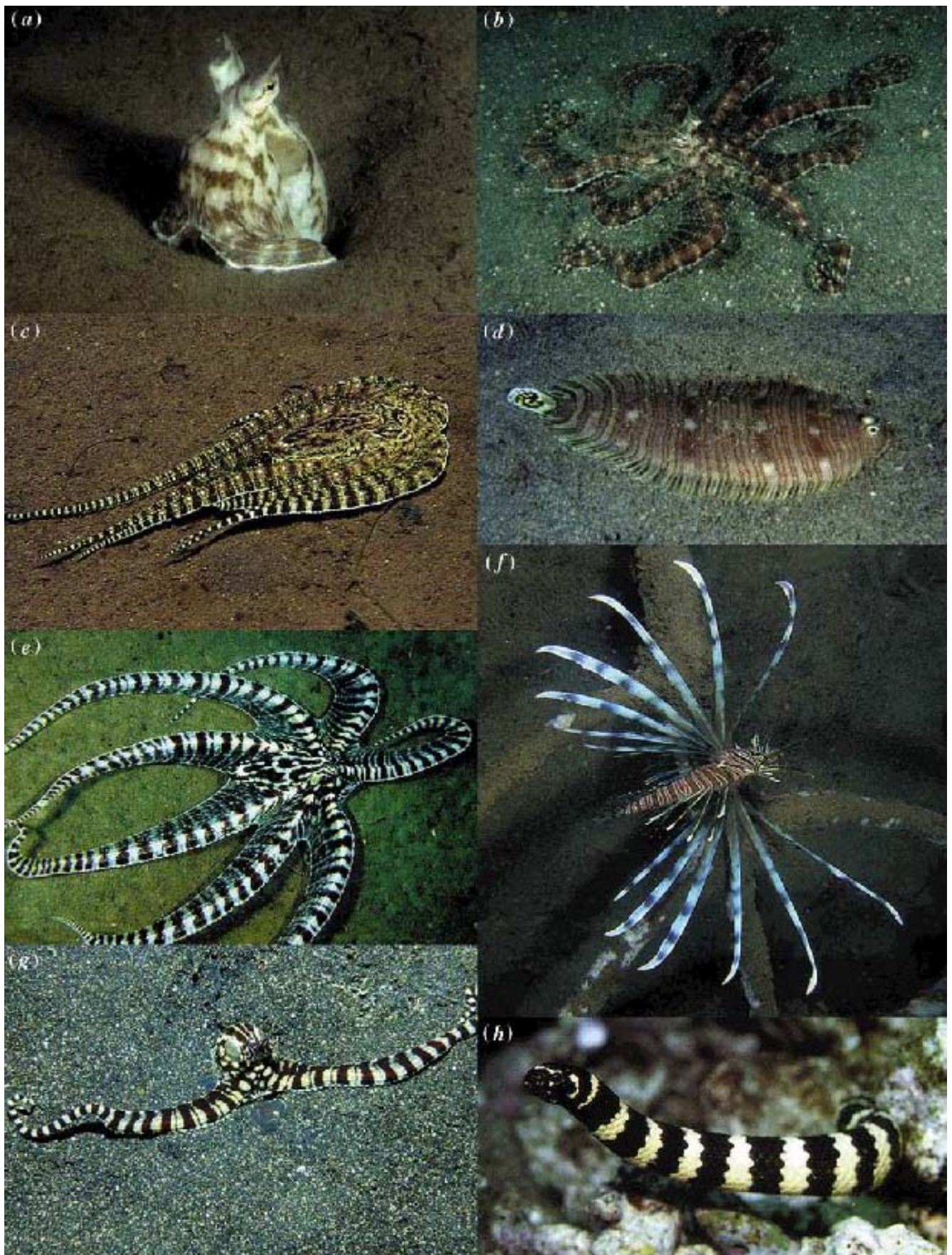


Figure 1. 'Mimic octopus': (a) sentinel state in mouth of burrow; (b) normal foraging colour pattern; (c) flatfish mimicry; (d) flatfish model, banded sole (*Zebrias* sp.); (e) lion-fish mimicry; (f) lion-fish model (*Pterois* sp.); (g) sea-snake mimicry; (h) sea-snake model, banded sea-snake (*Laticauda* sp.). Photographs by M. Norman and R. Steene.

behaviour may impersonate large jellyfishes found in the region.

All individuals were observed displaying more than one of the above behaviours. Human interpretations of potential mimics are subjective, and at this stage we are only confident in our interpretation of the mimicry of soles, lion-fishes and banded sea-snakes. Two individuals were observed employing all three of these forms of mimicry.

Unique foraging behaviour was also observed. In addition to typical speculative foraging (threading long arms down burrows and holes to seize fishes and crustacean prey), animals were observed to enter a tunnel completely and to emerge from another hole up to 1 m from the entrance point. We are unaware of any other octopuses that forage through subterranean tunnels.

4. DISCUSSION

In all putative examples of mimicry it is worth considering that the observed similarities may, in fact, be the product of convergent evolution. The mimic octopus may take on the appearance of a sea-snake simply because the same selective forces that make black-and-white bands a useful signal for the sea-snake also apply to the octopus. However, it seems very unlikely that such a remarkable resemblance of animals with radically different morphologies and behaviours is not due to mimicry.

It is striking that the most obvious impersonations by the mimic octopus are all of animals that produce strong toxins. Banded sea-snakes produce venom that is injected through fangs, the long bannered spines of lion-fishes are tipped with toxins, and soles (including *Zebrias* species) possess poison glands at the bases of the dorsal and anal fins.

Two points suggest that the mimic octopus is aiming to deceive predators: first, the models are toxic or dangerous, and second, their prey are mainly subterranean crustaceans and fishes. It is not known whether the mimic octopus is a poisonous (Müllerian) mimic or a non-toxic (Batesian) mimic. The latter possibility is supported by the fact that polymorphism in Müllerian mimics is rare (Turner 1984), and unlikely on theoretical grounds. This is because Müllerian mimics are expected to be subject to purifying selection to reduce the diversity of mimicry. Rare forms are strongly selected against, because predators are less likely to have learnt to avoid them. Müllerian mimicry might, therefore, tend to oppose the evolution of mimicry of multiple models. However, this assumes the simplest scenario, where all individuals in the mimicry complex have the same toxicity for all potential predators. If the situation is one in which there are differences in toxicity between models, and, more complex still, differences between predators in their sensitivities to the toxic properties of different mimics, then the strength of purifying selection will be reduced, potentially allowing multiple Müllerian mimicry to develop.

Although there does not seem to be any strong theoretical objection to the possibility that the mimic octopus is a Müllerian mimic, the fact that it regularly employs camouflage and predator-avoidance behaviour suggests that it is non-toxic to at least some of its potential predators. If the mimic octopus is non-toxic then its mimicry

can be regarded as Batesian, in which case selection is expected to favour the evolution of mimicry of a range of models, because novel forms of mimicry are less likely to be detected by predators and will tend to create a lower ratio of mimics to models. Mimicry of multiple models occurs through genetic polymorphism in a number of groups, notably papilionid butterflies and hoverflies (Mallet & Joron 1999), but in general is much less common than might be expected (Joron & Mallet 1998). One possible explanation for the rarity of polymorphic mimics is frequent selection towards the most noxious or abundant model (Turner 1984; Speed 1993). Alternatively, polymorphism may be rare because of the tight linkage between mimicry genes that is necessary to prevent recombination breaking up the coadapted complex. Unusual genetic architecture may be required to shift from one model to another (Charlesworth & Charlesworth 1975). The 'dynamic mimicry' (Norman *et al.* 1999) of the mimic octopus may escape this genetic constraint because it is not employed continuously: all individuals can carry alleles for all forms of mimicry simultaneously. This has been described as a 'neural polymorphism', whereby cephalopods gain the benefits of polymorphism, such as increased apparent rarity, without genetic polymorphism (Hanlon & Messenger 1996). The potential for a lower frequency of specific predator-morph encounters may also allow the octopus to use mimicry that is less accurate than that seen in species where permanent mimicry is employed. It is likely that dynamic mimicry is only possible due to several key attributes of cephalopods in general and octopuses in particular. The absence of a rigid internal or external skeleton reduces physical restrictions to adopting different shapes, and the octopus's ability to change the colour, pattern and shape of its skin makes it uniquely adapted to complex forms of mimicry.

Although it is likely that the mimic octopus's behaviour is the result of natural selection, it is worth considering the possibility that it may also be sexually selected. Complex behaviours may simply be courtship displays misinterpreted as mimicry. Alternatively, mimicry may have originally evolved as a result of selection for predator deterrence, but may now also be used in mate choice. There is evidence for sexual selection on song repertoire in various birds (for a review see Searcy 1992), and an analogous situation might occur in the mimic octopus if females prefer males with large impersonation repertoires. However, at present there is no evidence to support this possibility: both sexes show mimicry behaviour, all animals were well separated (50–100 m apart) and all displays were observed in the absence of conspecifics.

Although the potential for individuals to mimic more than one model may allow them to escape the genetic constraints associated with shifts in model, it does not fully explain how new forms of mimicry evolve. The evolution of new forms in the mimic octopus will depend on there being situations where a novel form of mimicry, even in an undeveloped form, is superior to the existing patterns that might be employed. For genetic polymorphisms the usual explanation is that rare morphs have higher fitness since there are fewer mimics relative to hosts. This may be the case in the mimic octopus, but there is a potential additional benefit of being able to mimic more than one model: dynamic mimicry has the

unique advantage that it can be employed facultatively, with the octopus adopting a form best suited to the perceived threat at any given time. Evidence for such sophisticated behaviour comes from our observation that on all occasions when sea-snake mimicry was observed it was exclusively a reaction to an attack by territorial damselfishes. Sea-snakes forage by entering burrows, and are predators of damselfishes (M. Norman, personal observation). The observation that the octopus uses a particular form of mimicry when it is most appropriate suggests that it is indeed able to use its powers of deception facultatively.

It is common for cephalopods to alter their appearance to match background patterns and textures (see review in Hanlon & Messenger 1996). Many species have been reported to impersonate distinct objects, such as rocks and coral (e.g. *Octopus cyanea*, Norman 2000), or plants, such as drift algae (e.g. *Sepioteuthis sepioidea*, Moynihan 1985). The only report of animal impersonation to date is that of the reef squid, *S. sepioidea*, impersonating the parrot-fish (Hanlon & Messenger 1996). In this case the mimicry is perhaps better described as background matching, as this disguise is typically employed by individual squid to 'hide' among foraging schools of parrot-fishes. No cephalopod species has previously been reported to impersonate individual animals in the absence of the model.

Given their remarkable morphological plasticity, it is perhaps puzzling that more examples of animal mimicry have not been reported in cephalopods. It may be that crypsis is generally a better anti-predator strategy for animals with such flexible body shapes and patterns. The open sand and mud habitat of the mimic octopus is a particularly exposed and predator-rich environment, and may explain why mimicry has evolved in this species. For an octopus to be active during daylight in such a habitat (with its lack of complex masking backgrounds) there may be strong selection for complex defence strategies. Octopuses lack the rapid escape capabilities of squids, and may have been able to occupy this foraging niche only through the evolution of complex mimicry.

The relatively limited research into the behaviour of cephalopods means that other examples of mimicry may

well be waiting to be discovered. Octopuses that are active during daylight on soft-sediment substrates may be interesting groups to target in the search for further examples of mimicry and other novel defensive strategies.

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An electronic appendix to this paper can be found at (<http://www.pubs.royalsoc.ac.uk>)